

PLANT SPECIES DISJUNCTIONS: A SUMMARY¹

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Disjunctions in the ranges of plant species have fascinated biologists ever since they were first detected; their interpretation has long been regarded as one of the central problems of plant geography. It seems intuitively reasonable that following its origin, a species should migrate to occupy a more or less continuous range; but when we find it occupying two or more areas separated by hundreds or even thousands of miles, we wonder how this pattern could possibly have originated. If the disjunction is expressed at a higher level—for instance, generic or familial—the problem remains the same, but its solution may be even more difficult.

Other papers in this symposium have touched on the major classes of disjunctions which have concerned biologists in the past. Before reviewing these, it is appropriate first to consider some general points that pertain to the study of all disjunctions and to consider some of the new and important kinds of evidence that have been brought into play in recent years.

GENERAL CONSIDERATIONS

In the study of disjunctions, as in all other questions of plant geography, an accurate taxonomic framework is a prerequisite, as stressed by Wood (this symposium). For example, the moss *Macromitrium sullivantii* C. Müll., thought to be an endemic of a small area of the southeastern Blue Ridge escarpment of the United States, has recently been shown to be identical with *Macrocoma hymenostomum* (Mont.) Grout, a well known species that occurs throughout the American tropics and South America (Anderson, 1970). The range as now understood becomes a striking example of a disjunct distribution. On the other hand, the genus *Boisduvalia* (Onagraceae), comprising six species of semiarid western North and South America, was until recently thought to include a species of the mountains of southeastern Australia and Tasmania, *B. tasmanica* (Hook. f.) Munz. With the demonstration that this species is actually an *Epilobium*, now known as *E. curtisiae* Raven, which forms natural hybrid populations with closely related Australian species (Raven, 1963a, and unpubl.), the situation demands a very different interpretation. In efforts to clarify the relationships between disjunct populations, the methods of chemosystematics (Hunziker *et al.*, Wagner, Turner, this symposium), biosystematics (*e.g.* Moore & Raven, 1970; Wagner, this symposium), and other modern techniques often have proven useful adjuncts to the more traditional morphological approaches (Wood, this symposium).

If one considers the distributions of plants throughout the world, one will be able to find examples of almost any conceivable sort of disjunct range. Thus very

¹ Support received from the U. S. National Science Foundation, most recently through Grant GB-29905, is gratefully acknowledged. D. I. Axelrod has kindly reviewed this manuscript.

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few genera of semiarid habitats are common to Australia and South America, but *Plagiobothrys* (Boraginaceae), *Calandrinia* (Portulacaceae), and *Nicotiana* (Solanaceae) exhibit this sort of range. The fact that *Nicotiana* also occurs on some Pacific islands (van Steenis & van Balgooy, 1966: 78-9) may provide a clue to its pathway of dispersal, but hardly justifies the construction of a landbridge across the tropical Pacific, as proposed for example by Corner (1963). Similarly, the occurrence of *Sibthorpia* (Rosaceae), *Hypochoeris* (Asteraceae), and *Deschampsia setacea* (Huds.) Hack. (Poaceae) in Europe and South America, but not in North America, must be taken as special cases and not used as the basis for postulating vast geological rearrangements.

Nevertheless, when considerable numbers of ranges coincide in their disjunctions, we are justified in looking for some collective reason. The recurrent disjunction between eastern Asia and eastern North America has been treated elegantly by Wood in the present volume; that between semiarid North and South America by Solbrig and by Turner; and the famous disjunction in range between some of the plants and animals of temperate South America and temperate Australasia has been mentioned by Culberson and by Schofield and Crum. For these and other equally impressive patterns, some historical explanation must be sought, but it must always be kept in mind that most patterns have been affected, sometimes profoundly, by Pleistocene events (Whitehead, this symposium).

At its simplest, a disjunction in range shows that there is some similarity between the habitats in the two disjunct areas. This fact in itself should serve as a warning when attempting to make summary judgments, for when two habitats are similar, there is always some probability of additional plants achieving the disjunction, regardless of its original historical basis (Simpson, 1952). For example, the disjunctions in range between *Nothofagus* (Fagaceae) and Proteaceae in temperate South America and Australasia are certainly related to Eocene geography, as we shall discuss below. On the other hand, to assert, as Melville (1966) does, that *Juncus scheuchzerioides* Gaud. (Juncaceae) achieved its range at such a remote time, is incredible. This species has dust-like seeds easily carried in the mud adhering to the feet of birds, and it occurs on many subantarctic islands known to have been completely glaciated in the Pleistocene. It is often possible to assign a maximum, but not a minimum, age to any particular example of disjunction, unless there is a fossil record (Whitehead, this symposium). Whenever two habitats are similar, they may have similar plants and animals, regardless of how far apart they may be, and additional ones may be added at a rate consistent with their powers of dispersal subsequently. Many plants have achieved striking disjunctions in range as weeds since the initiation of human activities on a global scale (Wagner, this symposium), and this is an indication of the sort of process that went on continuously before.

As in every human question, the explanation of disjunction may be strongly colored by the expectations and desires of the explainer. It is tempting to adduce only certain fractions of the evidence in the espousal of particular explanations, but it is unreasonable to expect these explanations to be correct for the whole. Each disjunction has its own explanation, and the reasons can be verified convincingly for the particular case only if there is a fossil record.

LONG-DISTANCE DISPERSAL

Islands such as Hawaii, Tahiti, and Samoa have never been connected with any continental area, and yet they have acquired significant numbers of plants and animals as a result of long-distance dispersal. In the case of Hawaii, the pattern of dispersal has been particularly well documented (Fosberg, 1948; Gemmell, 1954; Carlquist, 1967, 1970). South American bryophytes have spread to Tristan da Cunha, a million-year-old island in the middle of the South Atlantic (Schuster, 1969). On Marion and Prince Edward Islands, which lie in the Antarctic Ocean south of Africa and are no more than 276,000 years old, there occurs a flora of at least 80 species of mosses (van Zanten, 1971) and 36 liverworts (Grolle, 1971), including many "Antarctic relicts" that are often taken as evidence of continental drift. On these same islands, a pollen grain of *Nothofagus* that must have come about 7,500 km from South America was collected from snow (Schalke & van Zinderen Bakker, 1971). Similar patterns are evident in both the Arctic and the Antarctic (e.g. Young & Kläy, 1971), where recolonization of areas glaciated in the Pleistocene has taken place rapidly and recently.

In the face of these observations, it is clear that long-distance dispersal must also take place with a certain frequency in continental areas, despite the attempts of authors such as Crum (1972) to minimize its importance. If islands that have never been connected to continents have acquired certain animals and plants, then animals and plants with similar characteristics must be dispersed between areas on the mainland also. The characteristics of seed plants that are dispersed to islands have been discussed in an elegant essay by Carlquist (1967). The question is whether they will, once they have reached new areas, become established.

One of the most important aspects in the establishment and subsequent fate of a plant in a new locality is the breeding system of the population in question. Thus Baker (1955) pointed out the connection between self-compatibility and establishment following long-distance dispersal. In the present symposium, Schofield and Crum have considered the effect of dioicisism upon establishment by moss species, while Klekowski has stressed the genetic constitution of the sporophyte as related to the characteristics of the gametophyte in ferns. In both bryophytes (Crum, 1972) and ferns (Tryon, 1970), the spores are light and easily airborne for great distances; despite this, and also in the lichens (Culberson, this symposium), patterns of distribution, while perhaps somewhat broader on the whole, are strikingly like those observed in the flowering plants. In bryophytes and ferns, the gametophytes and sporophytes may demand different conditions for survival; and in both, gametophytes may occur far beyond the range in which sporophytes are normally produced in nature (Schofield & Crum, Wagner, this symposium). This is especially likely in dioicous mosses, for obvious reasons.

SEA-FLOOR SPREADING

During the past five years, the earth sciences have been the subject of a major revolution, as theories of plate tectonics have provided for the first time a basis sufficient to account for the kinds of movements of the continents first postulated

in 1915 by Wegener (Hammond, 1971*a*, 1971*b*). Since much of the information now generally accepted about the late Mesozoic and early Tertiary positions of the continents is of direct application to problems of disjunction in the ranges of plant taxa, it will be summarized briefly here.

Among the salient points that are emerging from this new synthesis are the early Cretaceous (110 m.y. BP) separation of South America from Africa, the middle Cretaceous (~ 90 m.y. BP) separation of Africa from Antarctica, the early to middle Eocene (55–47 m.y. BP) separation of Europe from North America, and the upper Eocene (45–49 m.y. BP) separation of South America and Australia from Antarctica (Dietz & Holden, 1970; Tarling, 1971; Raven & Axelrod, 1972). Some of the progressive climatic change that has taken place through the course of the Tertiary has been associated with sea floor spreading and changes in the position of the continents. For example, North America, Africa, and Australia have moved northward some 15° of latitude during the Cretaceous and Tertiary, and India some 50°, colliding with the mainland of Asia and throwing up the Himalayas in the process. All of these changes have had profound effects upon the disjunct distributions we observe at the present, as will be discussed below.

AGE OF TAXA INVOLVED IN DISJUNCTIONS

Increasing study of the fossil record has begun to provide valuable information on the probable age of angiosperm taxa, which can be brought to bear on problems of the age of particular disjunct ranges. For example, despite worldwide study and the common use of their pollen as indicators of particular strata, Asteraceae have not been identified in the fossil record before the lower Miocene, some 25 m.y. BP (Muller, 1970), and the tribe Cichorieae of this family not until the upper Miocene, about 10 m.y. BP (Couper, 1960). Too much evidence is available now to continue ignoring this fact, and it is scientifically inadmissible to continue attributing “antarctic” distributions of members of this family to dispersal across Antarctica during the Cretaceous or Eocene, more than 40 m.y. BP. Indeed, it is doubtful that *any* living sympetalous genus, with advanced pollination systems, existed early enough to have taken advantage of such a route of dispersal. The species of *Microseris* (Asteraceae—Cichorieae) that occur in western North America, western South America, and temperate Australasia can *only* have achieved their present ranges by long-distance dispersal, regardless of how improbable this may seem.

It is worth noting in passing that we have very little hard evidence about the rates of evolution of particular taxa, and it is extremely dangerous to reason from a given degree of morphological divergence to a length of time thought necessary to produce that divergence. If the Hawaiian honeycreepers (Drepanididae) could have differentiated from a common ancestor within a million years (Bock, 1970), why should we assume that the Hawaiian silverswords and their relatives (Asteraceae—Madiinae) have taken longer? On the other hand, certain plant species in Europe and western North America have scarcely changed since the late Eocene, some 40 m.y. (Axelrod, 1958, 1973)—much longer than the entire history of the family Asteraceae, in all likelihood. It is simply not justified to state that a certain degree of differentiation must have required a certain length of time, unless there

is a fossil record, yet arguments of this sort are commonplace in the literature on disjunct distributions.

MAJOR PATTERNS OF DISJUNCTION

Five major patterns of disjunction have been discussed repeatedly in the literature and mentioned frequently in the papers of this symposium. In addition, smaller disjunctions have been considered in other papers of this symposium and very often in the literature. The five major patterns distinguished here are treated in the sections that follow.

1. North Temperate Disjunctions

It has long been noted that many of the forest plants of the north temperate region have disjunct ranges, commonly between eastern Asia and eastern North America, but also involving western North America, southeastern Europe-Asia Minor and the mountains of eastern and southern Mexico. In the light of recent geological information, the long-standing explanation first proposed by Asa Gray, that of migration through the Bering Straits in times of milder climate, must be regarded as highly questionable. About 47–55 m.y. BP, in the early to middle Eocene, North America was still broadly joined to Europe from about 50°N latitude northward (Dietz & Holden, 1970). At this time Arcto-Tertiary forest vegetation was continuous across northern Europe and in much of western North America (Axelrod, 1973), and it is clear that the main migration path between Eurasia and North America was *via* Europe and the eastern United States (McKenna, 1972). By the start of the Tertiary (63 m.y. BP), the relationship between Asia and North America approached that of the present day (Pitman & Talwani, 1972; Churkin, 1972), so that migration into and out of North America was possible both from the east and from the west. The Bering Straits seem to have functioned as an important migration route between North America and Eurasia throughout the Tertiary (Simpson, 1947; Hopkins, 1967), although the geological history of Beringia needs further consideration in the light of plate tectonics.

If these relationships are as assumed above, the close similarity of Miocene floras in Japan, Alaska, and Oregon (Wolfe & Leopold, 1967) is not surprising. In the Cretaceous, there seems to have been a greater similarity between the pollen floras of eastern Asia and eastern North America than to any other part of the north Temperate zone; Muller (1970) has recognized an East Siberian-North Pacific pollen province and a North Atlantic-European one, reviewing the pertinent palynological literature. Smiley (1967) has considered Cretaceous leaf floras of Alaska to be closely similar to those of northeastern Siberia, although he later (Smiley, 1969) has stressed the homogeneity of the floras of the entire northern portion of Eurasia and North America at this time. These observations are consistent with the hypothesis of Churkin (1972), which places the west boundary of the North American continental plate in Yakutia, east Siberia. This suture is believed to have closed in early Cretaceous time. Nonetheless, direct migration *via* Europe apparently was feasible between Eurasia and North America into the early to middle Eocene (55–47 m.y.).

Disjunct ranges in the north temperate forest, excepting the rapid expansion

of Arctic species into formerly glaciated areas, are mainly Eocene in origin. For the boreal conifers, a more recent disjunction is implied. These relationships are interesting from an evolutionary point of view, because they imply that the related species of eastern Asia and the eastern United States have been evolving in isolation for approximately 47–55 m.y. As pointed out by Wood (this symposium), there are genera common to these two regions but very few species, a good indication of evolutionary rate in the groups concerned. Plants that are now found in various favorable areas of the north temperate zone have, in general, been separated by the deterioration of the climate in intervening areas; in this process, Pleistocene glaciation in Europe, with its east-west trending mountains, and the uplift of the Sierra Nevada-Cascade system in western North America have been important.

In evaluating such relationships, however, it is important to remember that for most of the Tertiary, the North Atlantic has been much narrower than at present, and probably was also dotted with islands. For many million years after the definitive separation of Europe and North America, birds probably flew back and forth regularly, and the probabilities of dispersal were very different from those obtaining at present. Some of the common species might have attained their disjunct ranges even more recently, as stressed by Wood (this symposium), as a result of long-distance dispersal; but it must be borne in mind that these are "closed" communities, where the chance of establishment may be relatively low, even if a seed does reach the disjunct area occasionally. For such entities as orchids, *Phryma leptostachya* L. (Verbenaceae), and *Circaea* (Onagraceae), all of which have readily dispersed seeds or fruits, it is difficult to imagine that they attained their disjunct ranges as early as the Eocene, and it would be dangerous to use their distributions to argue for or against such an antiquity for these plants.

One special disjunct pattern in the north temperate zone involves persistence in areas of mild oceanic climate, documented in this symposium by Culberson (for lichens), Schofield and Crum (for mosses), and Wagner (for ferns). Such ecological requirements have resulted in disjunctions between western North America and Europe, both onshore from warm oceanic currents. Patterns of this sort are rare or absent among the flowering plants.

2. East-west Desert and Mediterranean Disjuncts

Although there has always been a belt of reduced precipitation flanking the tropics, areas of desert and mediterranean climate in their present continental scale are a phenomenon of the past five million years (Axelrod, 1958, 1973; Raven & Axelrod, 1972). Some plant families that are restricted to semiarid or subhumid habitats have certainly been in existence since the Cretaceous, as pointed out by Rzedowski (1962) and others, but many species and genera confined to these areas have had a much more recent origin. In general, there is very little evidence for contact between the plants of the desert and mediterranean areas of North America and Eurasia (Raven, 1971, 1973a), despite the fact that these continents were broadly joined in the Eocene (Dietz & Holden, 1970; Tarling, 1971). This implies strongly that the plant associations involved were not in existence at the time, and also probably reflects the fact that the continents were joined

only at the north. It also suggests that the few genera and even fewer species common to the deserts and areas of mediterranean climate in the Old and New Worlds must have attained their present ranges by long-distance dispersal, a contention supported by the almost complete faunistic dissimilarity of the two areas. The several mosses (Schofield and Crum, this symposium) with this disjunction in range were almost certainly spread from one area to the other by long-distance dispersal.

3. Tropical Disjuncts

As reviewed by Axelrod (1970), there are many genera and infrafamilial taxa common to Africa and South America. Most of these presumably were present in the tropical vegetation of the two areas when they were contiguous in the early Cretaceous, or evolved in one or the other when the two continents were relatively near and partially connected by islands. Primary freshwater characoid fishes certainly spread overland between Africa and South America (Myers, 1967). On the other hand, present patterns of distribution suggest strongly that Cactaceae and Bromeliaceae evolved in South America subsequently, one genus of each having reached Africa, perhaps quite recently, by long-distance dispersal. If Bromeliaceae had been in existence in the Cretaceous, for example, it would be virtually unimaginable that they would not be represented in Africa at present. This strongly implies that the entire evolution of the family has taken place in the past 110 m.y. or less, a useful landmark in the fossil-poor monocots.

Many other plants have been dispersed between Africa and South America during the Tertiary, and they are doubtless still being dispersed at present. This possibility has been stressed recently by Iltis (1967) and others, and it would be a serious error to relate every disjunction between the continents to Cretaceous geography. In the lichen *Parmelia* subgen. *Amphigymnia*, discussed by Culberson (this symposium), it is especially difficult to date the time of dispersal between South America and Africa, in view of the presence of wind-dispersed soredia or isidia in many species; they may have been lost in others in the course of evolution.

Prior to the middle Tertiary, migration between subtropical areas in southeast Asia, India, and Africa has been simple and direct. Only with the late Tertiary development of the deserts of Arabia and the Near East has this communication been interrupted, and it is therefore not surprising to find many links between the floras of the Indo-Malaysian region and Africa. Madagascar, now known to have been separated from the coast of Somalia in the Cretaceous or more recently (Heirtzler & Burroughs, 1971), is the home of many relict plants and animals that have become extinct on the African mainland subsequently. Such survival accounts for the otherwise inexplicable similarities between the flora and fauna of Madagascar and the West Indies (Stearn, 1971) and between Madagascar and New Caledonia (Good, 1950).

Australasia, moving northward some 15° of latitude during the past 45–49 m.y., has approached tropical latitudes only within the past 10 million years, particularly with the emergence of New Guinea (Oligocene and subsequently; Raven & Axelrod, 1972). It has acquired its tropical flora during this period of time from the Indo-Malaysian region and as a result of the evolution of tropical representatives of archaic, austral groups of plants and animals as it moved northward.

4. Southern Hemisphere Temperate Disjunctions

Biologists have long been fascinated by the group of plants and animals that occupy disjunct ranges in the far-flung disjunct lands of the southern hemisphere. Many of these are related to the position of Australia and South America at the close of the Eocene, some 45–49 m.y. BP; both were directly connected with Antarctica (Dietz & Holden, 1970; Tarling, 1971; Raven & Axelrod, 1972). All three continents were occupied by a continuous cool temperate forest of gymnosperms and evergreen angiosperms that existed under equable conditions; in this forest were such plants as Podocarpaceae, Araucariaceae, Proteaceae, Winteraceae, Atherospermataceae, Epacridaceae, Loranthaceae, Myrtaceae, *Nothofagus*, and *Gunnera*, as well as many groups of lower plants and invertebrate animals that now have disjunct distributions in the south, including marsupials, hylid and leptodactylid frogs, and chelyid turtles, which crossed from South America to Australia by this route (review in Raven & Axelrod, 1972).

The gradual disruption of this once continuous forest by the movements of the continents was provided a predominant theme in southern hemisphere distributions. Some distributions, however, may be related to the earlier connection of Africa and India with Antarctica, broken during the middle Cretaceous. The austral gymnosperms (Florin, 1963), side-neck turtles, ratite birds, and galaxiid fishes (Darlington, 1948; Evans, 1958) seem to have reached Africa by this route, as did some leafy liverworts (Fulford, 1963). Among the angiosperms, there are a few patterns of distribution that suggest dispersal prior to the separation of Africa from Antarctica. Proteaceae, best developed in Australia, with closely related lines in South America and Asia and three very distinct lines in Africa, are suggestive of such a history (Johnson & Briggs, 1963); Xyridaceae and Restionaceae are also possible candidates (Cutler, 1972). It seems purely fanciful to relate the distributions of such living genera as *Gossypium* and *Solanum* (Hawkes & Smith, 1965), which provide no hint of such antiquity, to Cretaceous geography. Both genera have native species in Hawaii. The suggestion of Turner (this symposium) that the Centrospermae differentiated in a Gondwanaland that included Africa (= early Cretaceous) is almost ruled out by the Eocene origin of most families in this group (Muller, 1970). On the other hand, the families he discusses may well have differentiated in the south, after the separation of Africa, and subsequently spread to the northern hemisphere.

Many disjunct distributions involving southern lands, in contrast, are recent in origin (Moore, 1972); the case of *Juncus scheuchzerioides* and some other examples have already been mentioned. A number of plants that are easily dispersed by wind have doubtless been spread by the prevailing westerlies, seasonally four times as powerful as the corresponding winds in the northern hemisphere (Lamb, 1959). There is a great deal of evidence of such dispersal of small animals and seeds; recently data have been published which show that a balloon released at Christchurch, New Zealand, and held at approximately 40,000 feet elevation, made eight complete circuits of the southern hemisphere during 102 days (Mason, 1971). Other plants have been carried in the ocean currents (Sykes & Godley, 1968) or by birds (review in Raven & Axelrod, 1972; Raven, 1973b; see also Carlquist, 1970,

Chapter 4). Like all other disjunct distributions, ones between the southern lands must be taken with caution as indications of the age of the groups involved.

A single concrete example involves *Fuchsia* (Onagraceae), with more than 50 species in South America (northward to Mexico and the West Indies) and one section of four species in the Old World, three in New Zealand and one in Tahiti. It might at first be supposed that *Fuchsia* was a member of the Antarcto-Tertiary Geoflora and reached its disjunct stations overland via Antarctica, but four lines of evidence suggest that this was not the case: 1) the family Onagraceae may be no older than the middle Eocene (Muller, 1970); 2) *Fuchsia* first appears in the fossil record in New Zealand in the middle Miocene, fully 25 million years after the separation of Australasia from Antarctica, and it is not known from the fossil record in either Australia or Antarctica; 3) *Fuchsia* is bird-pollinated, both in the Old World and the New, and it is most unlikely that the specialized lines of birds that regularly visit and pollinate flowers were in existence much, if at all, before the Miocene; and 4) *Fuchsia* occurs on Tahiti, which stands in the middle of the Pacific and has never been connected to any land, a station it must have achieved by long-distance dispersal. In summary, the weight of evidence suggests strongly that *Fuchsia*, despite its occurrence in cool-temperate forest in both South America and New Zealand, attained its present disjunct distribution long after Antarctica was no longer available as a migration route, by means of long-distance dispersal across the Pacific.

5. Trans-Tropical Disjunctions

Disjunct distributions that span the tropics are not as likely to be remnants of formerly continuous distributions as the sorts of east-west disjunctions we have just discussed. Nevertheless, as Solbrig (this symposium) has indicated, there are opportunities for plants and animals of semiarid habitats to achieve only slightly interrupted ranges through the tropics even at the present day. Certain plants of temperate regions must also have passed through the tropics along elevated regions in the distant past, as suggested for example by the presence of *Nothofagus* as the only genus of Fagaceae in the southern hemisphere.

There are relatively few trans-tropical disjunctions involving Europe and Africa, presumably because the temperate area of South Africa is so limited. More disjunctions are known involving Asia and Australasia, and most of these seem quite recent in origin. Australasia has come into contact with Asia only in the upper Miocene, some 10 million years ago, and the mountains of Malaysia, New Guinea, Australia, and New Zealand were all uplifted in the Pliocene and later. Consequently, the migration paths visualized by van Steenis (1934a, 1934b, 1936) through Malaysia are no more than a few million years old, and the plants found on these mountains reached their disjunct stations mainly during the late Pliocene and Pleistocene by long-distance dispersal. Many north-temperate groups of plants reached Australia and New Zealand only at this time, and some have evolved rapidly in the newly opened subalpine and alpine habitats, particularly in New Zealand (Raven, 1972).

The best studied and most numerous transtropical disjuncts are those between North and South America, which have been in approximately their same relative

positions since at least the Cretaceous (Raven 1963*b*; Moore, 1972). Many of these involve identical or very closely related species of annual herbs in areas of mediterranean climate that were set up only in the late Pleistocene and subsequently (Moore & Raven, 1970; Raven, 1973*a*; Axelrod, 1973); there seems no doubt that most of these have achieved their disjunct ranges by direct, long-distance dispersal within the past several hundred thousand years. Each year during this time millions of individuals of the semipalmated plover, *Charadrius vulgaris*, have migrated between the areas that have disjunct plant species on the two continents, and these birds have provided at least one obvious means for direct long-distance dispersal (Cruden, 1966). Carlquist (1967) has convincingly demonstrated the probability of dispersal by birds as a means for achieving many of the disjunct distributions between North and South America, comparing these patterns with those involving dispersal to the Pacific Islands. Other plants have moved between North and South America by shorter jumps along the Andean chain, presumably in the main following its Pliocene uplift (Raven, 1973*a*).

Disjunctions on range between the plants of desert and other semiarid areas of North and South America have received considerable attention in this symposium (papers by Hunziker *et al.*, Solbrig, Turner). Even though areas of reduced precipitation have existed on the margins of the tropics since the beginnings of angiosperm evolution, and provided the initial site of evolution of many of the plant groups that occur in these deserts at the present time, the deserts themselves, in their present continental scale, are a phenomenon of the latest Tertiary (Axelrod, 1958). In other words, chances for dispersal between these areas, across the tropics or from east to west, are greater now than they have ever been at any time in the past (Axelrod, 1952). Solbrig has rightly re-emphasized the various times of dispersal that must have led to the many different patterns of disjunction at the present time. Some of the woody plants common to the deserts of North and South America have differentiated from tropical ancestors, whereas others extend more or less continuously through the tropics in "islands" of subhumid vegetation.

In general, the dissimilarity of the vegetation of semiarid areas in the Old and New World is a strong indication that many of the groups now involved in disjunctions in the New World were rare or not in existence in the Eocene. At any time subsequently, they may have become dispersed between North and South America, almost certainly in a series of steps. Drier sites in the tropics may have provided stepping stones by which such plants may have become dispersed throughout the Tertiary, but the fact that less than 2% of the desert floras of Argentina and the southwestern United States and adjacent Mexico are common to both areas makes it quite impossible to imagine a direct and simple pathway through the tropics, also not possible on climatic grounds. In addition, the insects and other animals of the two areas are almost entirely different, something that would not be true were there direct communication. The level of similarity that is actually observed is consistent with a sporadic, stepwise migration, operating at different times throughout the Tertiary and by different pathways, and resulting in a limited exchange of plant species and genera between North and South America. Detailed studies, such as that of Hunziker *et al.* (this symposium) on *Larrea* (Zygophyllaceae), will be necessary to clarify individual cases.

Concerning trans-tropical disjunctions, however, Florin's (1963) insistence on the long-sustained separation of north and south temperate floras still provides the most cogent generality. The uplift of mountains in the tropics of Africa, Malaysia, and America has facilitated movement between northern and southern hemisphere temperate areas, but such movement has apparently never been particularly easy, despite indications (*e.g.*, the origin of *Nothofagus*; podocarps and araucariads in the Tertiary of Europe) that it has continued throughout the entire history of angiosperms. During Pleistocene and Recent time, the great expansion of open semiarid habitats on both sides of the tropics has apparently provided conditions especially favorable for the establishment of some plants following long-distance dispersal, but the only appreciable exchange of this sort seems to have been that between North and South America, perhaps because these areas lie on regular migration paths of birds. There has been almost no corresponding exchange between semiarid regions of the Old and New Worlds except that brought about as a result of human activities. There is a considerable amount of bird migration between Eurasia and South Africa, but almost none that crosses Wallace's line into Australasia (McClure, 1971). Could this possibly be attributable to the relatively recent (15 m.y. BP) juxtaposition of Asia and Australia?

LITERATURE CITED

- ANDERSON, L. E. 1970. Geographical relationships of the mosses of the southern Appalachian Mountains. Virginia Polytech. Inst. Res. Div. Monogr. 2: 101-115.
- AXELROD, D. I. 1952. Variables affecting the probabilities of dispersal in geologic time. Bull. Amer. Mus. Nat. Hist. 99: 177-188.
- . 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. 24: 433-509.
- . 1970. Mesozoic paleogeography and early angiosperm history. Bot. Rev. 36: 277-319.
- . 1973. History of the Mediterranean ecosystem in California. In H. Mooney & F. DiCasti (editors), "Evolution of Mediterranean Ecosystems." In press.
- BAKER, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution 9: 347-348.
- BOCK, W. J. 1970. Microevolutionary sequences as a fundamental concept in macroevolutionary models. Evolution 24: 704-722.
- CARLQUIST, S. 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. Bull. Torrey Bot. Club 94: 129-162.
- . 1970. Hawaii. A Natural History. Garden City, New York.
- CHURKIN, M., JR. 1972. Western boundary of the North American continental plate in Asia. Geol. Soc. Amer. Bull. 83: 1027-1036.
- CORNER, E. J. H. 1963. *Ficus* in the Pacific region. In J. L. Gressitt (editor), "Pacific Ocean Biogeography." Pp. 233-245. Honolulu.
- COUPER, R. A. 1960. New Zealand Mesozoic and Cainozoic plant microfossils. New Zealand Geol. Surv. Paleont. Bull. 32: 1-88, pl. 1-12.
- CRUDEN, R. W. 1966. Birds as agents of long-distance dispersal for disjunct plant groups of the temperate Western Hemisphere. Evolution 20: 517-532.
- CRUM, H. 1972. The geographic origins of the mosses of North America's eastern deciduous forest. Jour. Hattori Bot. Lab. 35: 269-298.
- CUTLER, D. F. 1972. Vicarious species of Restionaceae in Africa, Australia and South America. In D. H. Valentine (editor), "Taxonomy, Phytogeography and Evolution," pp. 73-83.
- DARLINGTON, C. D. 1948. The geographical distribution of cold-blooded vertebrates. Quart. Rev. Biol. 23: 1-26, 105-123.
- DIETZ, R. S. & J. C. HOLDEN. 1970. Reconstruction of Pangaea: Breakup and dispersion of continents, Permian to present. Jour. Geophys. Res. 75: 4939-4956.
- EVANS, J. W. 1958. Insect distribution and continental drift. Univ. Tasmania Geol. Dept. Symp., Mar. 1956, p. 134-161.

- FLORIN, R. 1963. The distribution of conifer and taxad genera in time and space. *Acta Hort. Berg.* 20: 121-312.
- FOSBERG, F. R. 1948. Derivation of the flora of the Hawaiian Islands. In E. C. Zimmerman, "Insects of Hawaii." 1: 107-119. Honolulu.
- FULFORD, M. 1963. Continental drift and distribution patterns in the leafy Hepaticae. *Soc. Econ. Paleont. Mineral. Spec. Publ.* 10: 140-145.
- GEMMELL, A. R. 1954. Relationship and development of moss flora of Hawaii. VIII Congr. Internat. Bot., Vol. Prelim., pp. 90-91.
- GOOD, R. 1950. Madagascar and New Caledonia; a problem in plant geography. *Blumea* 6: 470-479.
- GROLLE, R. 1971. Hepaticopsida. In E. M. van Zinderen Bakker, Sr., J. M. Winterbottom & R. A. Dyer (editors), "Marion and Prince Edward Islands." Pp. 228-236. Cape Town.
- HAMMOND, A. L. 1971a. Plate tectonics: The geophysics of the earth's surface. *Science* 173: 40-41.
- . 1971b. Plate tectonics (II): Mountain building and continental geology. *Science* 173: 133-134.
- HAWKES, J. G. & P. SMITH. 1965. Continental drift and the age of angiosperms. *Nature* 207: 48-50.
- HEIRTZLER, J. R. & R. H. BURROUGHS. 1971. Madagascar's paleo-position: New data from the Mozambique Channel. *Science* 174: 488-490.
- HOPKINS, D. M. (editor). 1967. The Bering Land Bridge. Stanford.
- ILTIS, H. H. 1967. Studies in the Capparidaceae. XI: *Cleome afrospina*, a tropical African endemic with Neotropical affinities. *Amer. Jour. Bot.* 54: 953-962.
- JOHNSON, L. A. S. & B. G. BRIGGS. 1963. Evolution in the Proteaceae. *Austral. Jour. Bot.* 11: 21-61.
- LAMB, H. H. 1959. The southern westerlies: a preliminary survey; main characteristics and apparent associations. *Quart. Jour. Roy. Meteor. Soc.* 85(363): 1-23.
- MASON, B. J. 1971. Global atmospheric research programme. *Nature* 233: 383-388.
- MCCLURE, H. E. 1971. Some aspects of bird migration in Asia. *Rec. Proc. XII Pacif. Sci. Congr.* 1: 219-220.
- MCKENNA, M. C. 1972. Was Europe connected directly to North America prior to the middle Eocene? *Evol. Biol.* 6: (in press).
- MELVILLE, R. 1966. Continental drift, Mesozoic continents and the migrations of the angiosperms. *Nature* 211: 116-120.
- MOORE, D. M. 1972. Connections between cool temperate floras, with particular reference to southern South America. Pp. 115-138, in D. H. Valentine (editor), "Taxonomy, Phyto-geography and Evolution."
- & P. H. RAVEN. 1970. Cytogenetics, distribution and amphitropical affinities of South American *Camissonia* (Onagraceae). *Evolution* 24: 816-823.
- MULLER, J. 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev. Cambridge* 45: 417-450.
- MYERS, G. S. 1967. Zoogeographical evidence of the age of the south Atlantic Ocean. *Stud. Trop. Oceanogr. Miami* 5: 614-621.
- PITMAN, W. C. & M. TALWANI. 1972. Sea floor spreading in the North Atlantic. *Bull. Geol. Soc. Amer.* 83: 619-646.
- RAVEN, P. H. 1963a. The generic position of "*Boisduvalia tasmanica*." *Aliso* 5: 247-249.
- . 1963b. Amphitropical relationships in the floras of North and South America. *Quart. Rev. Biol.* 38: 151-177.
- . 1971. The relationships between 'mediterranean' floras. In P. H. Davis, P. C. Harper & I. C. Hedge (editors), "Plant Life of South-West Asia," pp. 119-134. Edinburgh.
- . 1972. Evolution and endemism in the New Zealand species of *Epilobium*. Pp. 259-274, in D. H. Valentine (editor), "Systematics, Phytogeography and Evolution."
- . 1973a. The evolution of 'mediterranean' floras. In H. Mooney & F. DiCasteri (editors), "Evolution of Mediterranean Ecosystems." In press.
- . 1973b. The evolution of subalpine and alpine plant groups in New Zealand. *New Zealand Jour. Bot.* (in press).
- & D. I. AXELROD. 1972. Plate tectonics and Australasian paleobiogeography. *Science* 176: 1379-1386.
- RZEDOWSKI, J. 1962. Contribuciones a la fitogeografia floristica e historia de México. I.

- Algunas consideraciones acerca del elemento endémico en la flora mexicana. *Bol. Soc. Bot. Méx.* 27: 52-65.
- SCHALKE, H. J. W. G. & E. M. VAN ZINDEREN BAKKER, SR. 1971. History of the vegetation. In E. M. van Zinderen Bakker, Sr., J. M. Winterbottom & R. A. Dyer (editors), "Marion and Prince Edward Islands," p. 89-97. Cape Town.
- SCHUSTER, R. M. 1969. Problems of antipodal distribution in lower plants. *Taxon* 18: 46-91.
- SIMPSON, G. G. 1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. *Bull. Geol. Soc. Amer.* 58: 613-688.
- . 1952. Probabilities of dispersal in geological time. *Bull. Amer. Mus. Nat. Hist.* 99: 163-176.
- SMILEY, C. J. 1967. Paleoclimatic interpretations of some Mesozoic floral sequences. *Amer. Assoc. Petrol. Geol. Bull.* 51: 849-863.
- . 1969. Cretaceous floras of Chandler-Colville region, Alaska: Stratigraphy and preliminary floristics. *Amer. Assoc. Petrol. Geol. Bull.* 53: 482-502.
- STEARNS, W. T. 1971. A survey of the tropical genera *Oplonia* and *Psilanthele* (Acanthaceae). *Bull. Brit. Mus. Nat. Hist. Bot.* 4: 261-323, pl. 38-47.
- STEENIS, C. G. G. J. VAN. 1934a. On the origin of the Malaysian mountain flora. i. Facts and statement of the problem. *Bull. Bot. Gard. Buitenzorg III.* 13: 139-262.
- . 1934b. On the origin of the Malaysian mountain flora. 2. Altitudinal zones, general considerations and a renewed statement of the problem. *Bull. Bot. Gard. Buitenzorg III.* 13: 289-417.
- SYKES, W. R. & E. J. GODLEY. 1968. Transoceanic dispersal in *Sophora* and other genera. *Nature* 218: 495-496.
- . 1936. On the origin of the Malaysian mountain flora. 3. Analysis of floristic relationships. Pt. i. The Sumatran track. *Bull. Bot. Gard. Buitenzorg III.* 14: 56-72.
- & M. M. J. VAN BALGOOY (editors). 1966. *Pacific Plant Areas*. Vol. 2. *Blumea Suppl.* Vol. 5: 1-312.
- TARLING, D. H. 1971. Gondwanaland, palaeomagnetism, and continental drift. *Nature* 229: 17-21.
- TRYON, R. 1970. Development and evolution of fern floras of oceanic islands. *Biotropica* 2: 76-84.
- WEGENER, A. 1915. *Die Entstehung der Kontinente und Ozeane*. Sammlung Vieweg, Brunswick; No. 20.
- WOLFE, J. A. & E. B. LEOPOLD. 1967. Neogene and early Quaternary vegetation of northwestern North America and northeastern Asia. In D. M. Hopkins (editor), "The Bering Land Bridge," pp. 193-206. Stanford.
- YOUNG, S. B. & J.-R. KLÄY. 1971. Bryophytes in the 1969 crater of Deception Island, Antarctica: An apparent case of rapid long-distance dispersal. *Ohio Jour. Sci.* 71: 358-362.
- ZANTEN, B. O. VAN. 1971. Musci. In E. M. van Zinderen Bakker, Sr., J. M. Winterbottom & R. A. Dyer (editors), "Marion and Prince Edward Islands," pp. 173-227. Cape Town.